THE GAS CONTENT OF THE SWIMBLADDER OF THE ROCK BASS, AMBLOPLITES RUPESTRIS, IN RELATION TO HYDROSTATIC PRESSURE

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Introduction

A number of years ago Haldane suggested that the gases in the swimbladder of a physoclistomous fish are of blood origin; i.e., they are secreted into the swimbladder. Evidence has been secured in favor of such an hypothesis by Hall (1924), Powers (1932), Von Ledebur (1937), and Black (1940). However, Krogh (1941) states, "This suggestion is very plausible, but even if proved would not go far to explain the gas secretion in this organ." The work of Powers, Jacobs, and Meesters and Nagel suggests the fundamental rôle of carbon dioxide in the physiology of the swimbladder. Perhaps it is necessary to know the limits of hydrostatic adjustment, the effect of barometric pressure changes on the general physiology of the fish, and the relation between the partial pressures of the gases in the swimbladder and the hydrostatic pressure before the physiology of the rete mirabile and the gas gland can be thoroughly understood. Many facts concerning the physiology of the swimbladder must be known before the rôle of this organ can be definitely established in the adjustment of fish to adverse conditions at certain levels, in the adjustment to barometric pressure changes, and the failure of adjustment in "sudden" mortality of fish during times of lake turnover.

The work presented below was performed with the hope of establishing a basis for further work toward the possible solution of these problems.

Apparatus and Method

An apparatus for the accurate control of hydrostatic pressure was designed, which consisted of a steel tank with a capacity of 32 gallons and capable of withstanding a pressure of 180 pounds. The tank was fitted with two 1½-inch, two 1-inch, and two half-inch tappings, a "sight glass" of vellemoid glass 2½ inches in diameter, and one hand-hole. The interior of the tank was lighted with a 40-watt bulb inclosed in an explosion-proof globe purchased from the Crause-Hinds Company of Syracuse, New York. Pressure was maintained by a piston pump, the model " Marvel " constructed by the Deming Pump Company of Salem, Ohio. Under the experimental conditions the capacity of this pump was approximately two gallons per minute.

Pressure below one atmosphere was obtained by connecting the outlet of the tank to the pump, and the inlet to the lake. A by-pass was placed between the tank and the pump. Valves were placed between the tank and lake, tank and pump, and in the by-pass leading to the lake. The tank was filled completely with water, closed, and the pump started

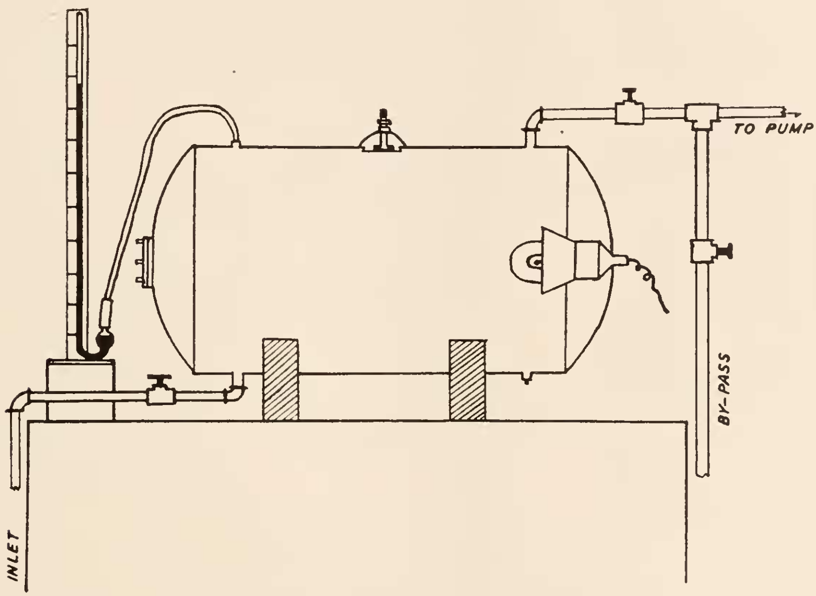

FIG. 1. Diagram of experimental apparatus, showing the arrangement used to produce pressure below one atmosphere.

with the by-pass open. When the pump had reached its capacity the by-pass was closed, and all the water was sucked from the lake through the tank. With this arrangement a pressure of 540 mm. Hg, equal to an altitude of 8,000 ft., was obtained. Figure 1 shows the arrangement of connections necessary to obtain this pressure.

The apparatus was thoroughly checked for air leaks by analyzing samples of water from the tank on the Van Slyke Blood Gas Analysis Apparatus and comparing with the analysis of samples taken from the open lake from which the water was pumped. In no case was there evidence that air was being forced into the water by the pump. The gaseous content of the lake water remained practically constant throughout the experimental period (See Table I).

Hydrostatic pressure was measured by a gauge which was calibrated before the experiments were carried out and checked again at the end of the work. Low pressures were measured by means of a mercury manometer.

Gas was removed from the swimbladders of the experimental fish by an apparatus which consisted of two tonometers, a leveling bulb, and a hypodermic needle. The second tonometer was filled with mercury, as was the needle and its connection, and a partial vacuum was created in the first tonometer. The hypodermic needle was then inserted into the lumen of the swimbladder, the stopcocks opened, and gas was sucked into the second tonometer. All gas samples were removed while the

TABLE I

Analyses of the oxygen and nitrogen in the lake water compared with the amounts of these gases in the water of the tank at the time of the experiment.

No. Exp.	Average Pressure in Tank	O_2 in Tank	O_2 in Lake	N_2 in Tank	N_2 in Lake
	mm. Hg	*vol. per cent*	*vol. per cent*	*vol. per cent*	*vol. per cent*
6	761	.57	.52	1.13	1.11
12	2218	.77	.73	1.26	1.23
14	2229	.59	.71	1.11	1.18
19	1420	.67	.72	1.12	1.14
20	1147	.60	.60	1.33	1.33
24	1153	.72	.77	1.09	1.12
25	996	.91	.81	1.08	1.08
27	540	.79	.72	1.26	1.30
28	540	.79	.77	1.35	1.32

fish were submerged. The gas was analyzed by the use of the Henderson-Bailey Modification of the Haldane Apparatus.

The rockbass, *Ambloplites rupestris,* was selected as the experimental animal because it has a closed type of swimbladder, survives handling well, and recovers quickly from pressure effects. The blood of this fish is perhaps better buffered than such species as sheepshead and perch (Powers et al, 1939). The rockbass survives relatively high tensions of carbon dioxide.

The experimental procedure was as follows. Three rockbass, which had been removed from a shallow live-box where they had been confined for two days, were placed in the tank and the pressure was gradually increased to the point desired, where it was maintained until the fish had reached a state of hydrostatic equilibrium. This condition is defined as being that state in which the fish make little effort to maintain their position; i.e., they swim on an even keel. When it was evident that this condition had been established (by observation through the "sight glass"), the fish were removed from the tank and gas samples were taken, usually within two minutes after the fall of pressure.

Discussion of Experimental Data

Determinations of the swimbladder gas contents were made on fish which had been subjected to the following total pressures (hydrostatic plus atmospheric): 540 mm. Hg, 751 mm. Hg, 760 mm. Hg, 996 mm. Hg, 1148 mm. Hg, 1417 mm. Hg, and 2223 mm. Hg. The fish were removed from the tank when they had established a state of hydrostatic equilibrium. Several experiments were carried out at each pressure level, and as there were usually slight differences in pressure, the above pressures are averages. The data of the experiments are tabulated in Table II. The results obtained from the analyses of swimbladder gas taken from fish subjected to 750 and 751 mm. Hg are designated "controls." Those obtained at 760 mm. Hg were the results of analyses of swimbladder gas taken from fish which were removed from a live-box where they had been kept for at least two days. The results at 750 mm. Hg were obtained from fish which had been placed in the tank for six hours with no pressure registering, but with a constant flow of water passing through the tank. The average percentage of carbon dioxide in the swimbladders of fish taken from the live-box was 2.02 per cent, and 1.54 per cent in the case of the fish placed in the tank for six hours. The oxygen percentage in the "control" experiment at 750 mm. Hg was 14.98 per cent, while the percentage of oxygen in the swimbladder of fish taken from the live-box was 15.93 per cent, on the average. The nitrogen in the "control" was 83.63 per cent, and in the fish taken from the live-box the percentage of nitrogen was 81.92 per cent.

At the suggestion of Dr. Alfred C. Redfield, a constant volume of the swimbladder was assumed for fish in a state of hydrostatic equilibrium at any hydrostatic pressure. For example, fish subjected to 750 mm. Hg pressure, the "control," were assumed to have a certain volume of the swimbladder, and fish which were in a state of hydrostatic equilibrium at 996 mm. Hg would have the same volume which they had at 750 mm. Hg, since the density of the fish is equal to the density of the water, and the mass of the fish is unchanged when the fish have reached a state of hydrostatic equilibrium. This assumption gives a basis for calculating the volume of each gas, the gain or loss of each gas in the swimbladder in making the equilibration from the level of the "control," and the rate of gas deposition at each pressure level. In Table III the milliliters of each gas in 100 ml. of swimbladder gas at a given hydrostatic pressure is corrected to normal conditions of temperature and pressure, that of the " control."

The results at the various pressure levels will be discussed with reference to the volume of each gas at normal temperature and pressure, beginning at the reduced pressure of 540 mm. Hg. When fish had

TABLE II

Results of the analyses of swimbladder gas obtained from the rockbass, Ambloplites rupestris, which had attained a state of hydrostatic equilibrium at the total pressures given in column No. 2.

No. Exp.	Total Pressure	Time	Temp. of Water	CO_2	O_2	N_2
	mm. Hg	*hours*	*° C.*	*per cent*	*per cent*	*per cent*
26	540	24	26.4	0.85	3.94	95.21
27	540	24	26.4	0.73	6.37	92.93
28	540	22.5	25.5	0.75	4.22	95.02
28	540	22.5	25.5	0.72	4.78	94.49
28	540	22.5	25.5	0.72	4.19	95.08
av.	540	23	26	0.77	4.50	94.54
1	750	6.0	11.6	1.23	14.79	83.98
1	750	6.0	11.6	1.54	13.50	84.96
1	750	6.0	11.6	1.79	16.20	82.21
2	751	6.0	13.9	.97	10.01	89.02
2	751	6.0	13.9	1.91	17.98	80.11
2	751	6.0	13.9	1.67	16.30	83.03
3	751	6.0	15.5	1.81	18.94	79.25
3	751	6.0	15.5	1.42	13.10	86.48
av.	750	6.0	13.6	1.54	14.98	83.63
32	759	l.b.*	21.6	1.15	18.17	80.68
32	759	l.b.	21.6	1.87	20.87	77.26
6	761	l.b.	22.2	3.37	13.68	82.44
6	761	l.b.	22.2	1.67	11.02	82.31
av.	760		22.0	2.02	15.93	81.92
25	996	10.5	26.6	6.73	37.11	56.12
25	996	10.5	26.6	3.02	35.08	61.89
25	996	10.5	26.6	4.66	25.86	69.46
av.	996	10.5	26.6	4.73	32.68	61.26

* l.b., live box.

reached hydrostatic equilibrium at 540 mm. Hg, it was found that all gases had been partially removed from the swimbladder. At this pressure the amount of carbon dioxide in 100 ml. of swimbladder gas was only 0.7 ml., and the amount of oxygen on the same basis was only 4.5 ml., while the nitrogen in 100 ml. of swimbladder gas was 94.5 ml. When corrected to normal conditions of temperature and pressure, the above volumes become 0.5 ml. CO_2, 3.1 ml. O_2, and 65 ml. N_2. The amounts of each gas in 100 ml. of swimbladder gas removed from fish in the "control" at 750 mm. Hg and 13.6° C. are 1.5 ml. CO_2, 15.0 ml. oxygen, and 83.6 ml. nitrogen. Thus it can be seen that one milliliter of carbon dioxide per 100 ml. of swimbladder gas has been lost along with 11.9 ml. of oxygen and 17.6 ml. of nitrogen. (Table III gives the milliliters of each gas gained or lost per 100 ml. of swimbladder gas in

TABLE II—*Continued*

No. Exp.	Total Pressure	Time	Temp. of Water	CO_2	O_2	N_2
	mm. Hg	*hours*	*° C.*	*per cent*	*per cent*	*per cent*
20	1147	24.1	25.5	16.45	35.67	47.88
21	1145	23.7	26.1	3.50	45.28	51.20
21	1145	23.7	26.1	8.29	44.50	47.20
21	1145	23.7	26.1	9.36	34.38	55.81
24	1153	25.1	25.5	15.24	35.22	49.45
24	1153	25.1	25.5	11.88	36.92	51.13
25	1153	25.1	25.5	4.46	39.60	55.94
av	1147	24.4	25.5	9.88	38.86	51.24
19	1420	38.5	26.1	6.69	51.60	41.71
19	1420	38.5	26.1	13.24	46.89	39.79
19	1420	38.5	26.1	11.80	32.17	55.83
5	1414	47.5	22.2	15.27	42.24	42.23
5	1414	47.5	22.2	11.27	40.89	46.84
5	1414	47.5	22.2	2.35	56.85	40.80
av.	1417	43.0	24	10.17	45.10	44.53
12	2218	56.5	21.6	8.43	55.57	36.00
12	2218	56.5	21.6	7.40	61.30	31.31
12	2218	56.5	21.6	8.53	60.26	31.14
13	2223	56.5	21.6	7.97	62.17	29.92
13	2223	56.5	21.6	10.99	42.07	46.94
14	2229	66.5	25	9.02	52.05	35.35
14	2229	66.5	25	9.75	45.90	43.35
14	2229	66.5	25	8.39	61.18	40.48
av.	2223	61.0	22.6	8.96	54.73	36.31

equilibrating to the various levels of hydrostatic pressure.) In order to reach equilibrium at 540 mm. Hg, approximately 27 per cent of the gas in the swimbladder at equilibrium at 750 mm. Hg would have to be removed. Since only 5 per cent of the gas at 750 mm. Hg is carbon dioxide and oxygen, equilibrium at 540 mm. Hg cannot take place unless nitrogen is removed. Unless nitrogen is removed, the rockbass could not come to equilibrium at a pressure of less than 635 mm. Hg. Brown (1939) offers experiments on the guppy as evidence of nitrogen deposition at reduced pressures. The results on the rockbass do not show nitrogen deposition in the adjustment to any pressure, as will be pointed out below. However, Brown found that the guppy did not make adjustment to pressure reductions of more than 125 mm. Hg. If the swimbladder, as stated above, did not contain more than 16 per cent carbon dioxide plus

TABLE III

The milliliters of each gas gained or lost per 100 ml. of swimbladder gas were calculated from the data secured at each pressure level as given in Table II, assuming a constant volume of the swimbladder at hydrostatic equilibrium.

Average Total Pressure	CO_2	O_2	N_2	
mm. Hg	*ml*	*ml*	*ml*	
540	0.7	4.5	94.5	per 100 ml.
	0.5	3.1	65.0	corrected NTP
	−1.0	−11.9	−17.6	gain or loss
750	1.5	15.0	83.6	"Control" NTP = 750 mm. Hg, 13.6° C.
760	2.0	15.9	81.9	per 100 ml.
	1.9	15.6	86.4	corrected NTP
	+0.4	+0.6	−3.2	gain or loss
996	4.7	32.7	61.3	per 100 ml.
	6.0	41.5	78.8	corrected NTP
	+4.5	+26.5	−4.8	gain or loss
1147	9.9	38.9	51.2	per 100 ml.
	14.5	57.3	75.3	corrected NTP
	+13.0	+42.3	−8.3	gain or loss
1417	10.2	45.1	44.5	per 100 ml.
	18.3	81.9	80.6	corrected NTP
	+16.8	+66.9	−3.0	gain or loss
2223	8.9	54.7	36.3	per 100 ml.
	25.6	156.5	103.8	corrected NTP
	+24.1	+141.5	+20.2	gain or loss

oxygen, adjustment could not be made to pressures below 635 mm. Hg without the removal of nitrogen.

In the adjustment to 996 mm. Hg it was found that 4.5 ml. carbon dioxide and 26.5 ml. oxygen were deposited in the swimbladder while 4.8 ml. nitrogen were removed for every 100 ml. of swimbladder gas.

At hydrostatic equilibrium at the total pressure of 1147 mm. Hg there were deposited in the swimbladder 13 ml. carbon dioxide and 42.3 ml. oxygen; and 8.3 ml. nitrogen were removed per 100 ml. of swimbladder gas.

The adjustment to the hydrostatic pressure of 1417 mm. Hg was the result of the deposition of 16.8 ml. carbon dioxide and 66.9 ml. oxygen per 100 ml. of swimbladder gas, while 3 ml. of nitrogen were removed.

Likewise there was a deposition of 24.1 ml. carbon dioxide and 141.5 ml. oxygen per 100 ml. of swimbladder gas in the adjustment to 2223 mm. Hg pressure. In this case nitrogen appeared to have increased. The slight deviation of the nitrogen in several experiments from the level of the " control " is believed to be due to an error in the use of average figures, originally caused by the failure of some fish in the experiment to have reached complete equilibrium.

Figure 2 is a graphic representation of the data compiled in Table III in which the milliliters of the three gases per 100 ml. of swimbladder gas are plotted against the hydrostatic pressure in mm. Hg. It can be seen that the nitrogen fluctuates only slightly. It will be noted that the volume of carbon dioxide plotted against the hydrostatic pressure forms a curve which tends to level off as the pressure increases. The oxygen forms a nearly straight line, which indicates that the deposition of this gas is largely responsible for the adjustment to hydrostatic pressure. At the total pressure of 2223 mm. Hg, over half of the pressure exerted against the swimbladder wall is due to oxygen. Carbon dioxide partial pressure (200 mm. Hg) is equal to only one-tenth of the total pressure. Meesters and Nagel (1934–35) state that 86 per cent of the " Ersatzegase " is composed of carbon dioxide. Their results were obtained for only the first hour of gas deposition. If the gas entering the swimbladder is composed of 86 per cent carbon dioxide for the duration of gas deposition, carbon dioxide partial pressure would be much higher than 200 mm. Hg. In as much as the pressure of oxygen at 2223 mm. Hg is half the total pressure, it is impossible that the secretion of carbon dioxide continued to form 86 per cent of the total secretion and it is quite likely that the ratio of carbon dioxide to oxygen secreted changes greatly during equilibration. The ratio of these two gases varies considerably at equilibrium. In Table IV the milliliters of carbon dioxide and oxygen are the corrected volumes of these gases in 100 ml. of swimbladder gas observed at equilibrium at the various pressure levels.

The average ratio is 6.5; i.e., there are 6.5 times more oxygen than carbon dioxide in the swimbladder at hydrostatic equilibrium. Meesters and Nagel found 6.1 times more carbon dioxide than oxygen in the gas which entered the swimbladder during the first hour of gas deposition.

Two series of experiments were performed which cast some light on the rate of gas deposition, the rôle of carbon dioxide after the first two hours of gas deposition, and upon the relation of the amount of carbon

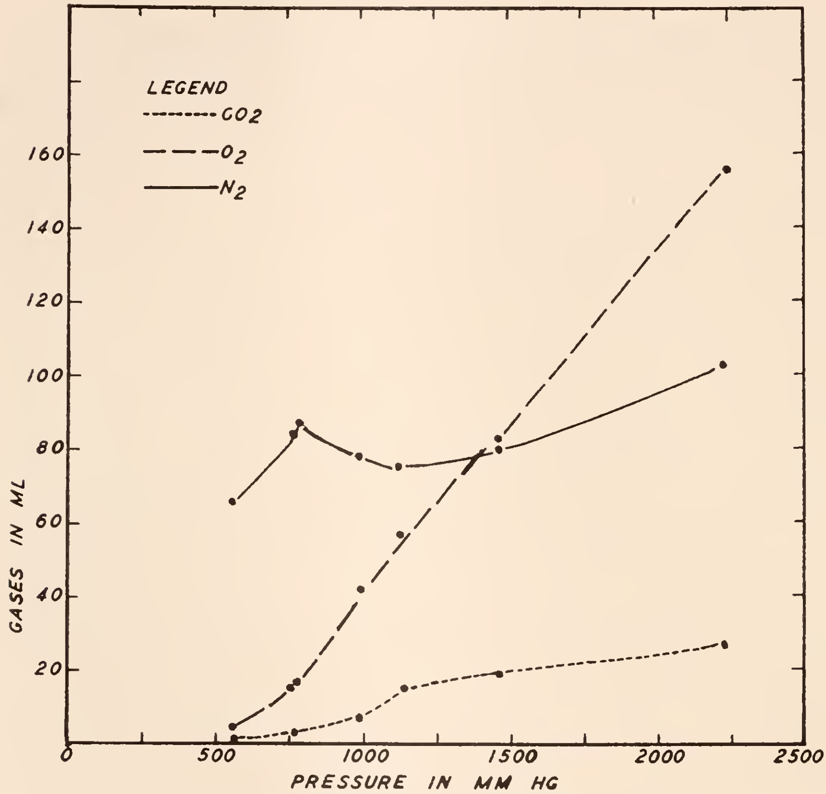

FIG. 2. A graphic representation of the data of Table III wherein the volume of gas is calculated on the assumed volume of 100 ml. for the swimbladder at hydrostatic equilibrium.

dioxide deposited to the strength of the stimulus—the hydrostatic pressure. In one series of experiments the pressure, 996 mm. Hg, remained constant, and the fish were placed under this pressure for various lengths of time. The results of analyses of swimbladder gas taken from fish which had been subjected to 996 mm. Hg for two hours, 10.5 hours, and

TABLE IV

Hydrostatic Pressure	CO_2	O_2	Ratio O_2/CO_2
mm. Hg	*ml.*	*ml.*	
540	0.5	3.1	6.2
750	1.5	15.0	10.0
760	1.9	15.6	8.2
996	6.0	41.5	6.9
1147	14.5	57.3	3.9
1417	18.3	81.9	4.4
2223	25.6	156.5	6.1

24.6 hours are given in Table V. Figure 3 is a graphic representation of these data wherein the partial pressures of the various gases are plotted against "time." It can be seen that the partial pressure of carbon dioxide is rapidly increased, from the point of the "control" during the first two hours. The "control" is the average amount of carbon dioxide in the swimbladder of fish at the surface of the lake. The rate of increase of carbon dioxide falls off during the next eight hours. When the fish are allowed to remain at this pressure (996 mm. Hg) for 24.6 hours, which is 12.5 hours after they have reached a state of hydrostatic equilibrium, carbon dioxide partial pressure has decreased by

TABLE V

These data were obtained from analyses of swimbladder gas taken from fish which had been subjected to 996 mm. Hg hydrostatic pressure for the durations listed in column No. 2.

No. Exp.	Time	Total Pressure	CO_2 Content	CO_2 Pressure	O_2 Content	O_2 Pressure	N_2 Content	N_2 Pressure	Temp. of Water
	hours	*mm. Hg*	*per cent*	*mm. Hg*	*per cent*	*mm. Hg*	*per cent*	*mm. Hg*	°*C.*
29	2.0	993	7.65	74.2	25.70	248.3	66.66	644.0	26.8
29	2.0	993	3.42	33.0	17.30	167.1	79.26	765.7	26.8
29	2.0	993	1.01	9.7	26.60	256.9	72.39	699.3	26.8
av.			4.03	39.0	23.20	204.5	72.81	703.0	
25	10.5	996	6.73	64.6	37.11	353.6	56.12	559.3	25.8
25	10.5	996	3.02	29.0	35.08	337.1	61.89	594.7	25.8
25	10.5	996	4.66	44.7	25.86	248.5	69.46	677.5	25.8
av.			4.73	46.1	32.68	325.1	61.26	610.5	
23	24.6	999	2.13	20.8	31.27	305.9	66.60	651.5	22.7
23	24.6	999	3.81	37.2	35.22	344.5	60.96	596.4	22.7
23	24.6	999	2.06	20.1	45.45	444.5	52.46	513.2	22.7
av.			2.67	26.0	37.33	365.0	60.00	587.0	

two-fifths of its value at 10.5 hours. Concomitantly with the rise in carbon dioxide, there is an 8 per cent increase in oxygen during the first two hours of stimulation. During the next eight hours the oxygen increased 12 per cent, while only 2 per cent increase was shown for this gas during the last 14 hours. It has been suggested by Dr. Laurence Irving [1] that the delay in the maximum of oxygen in contrast to carbon dioxide in the swimbladder may be due to the relatively large volume of

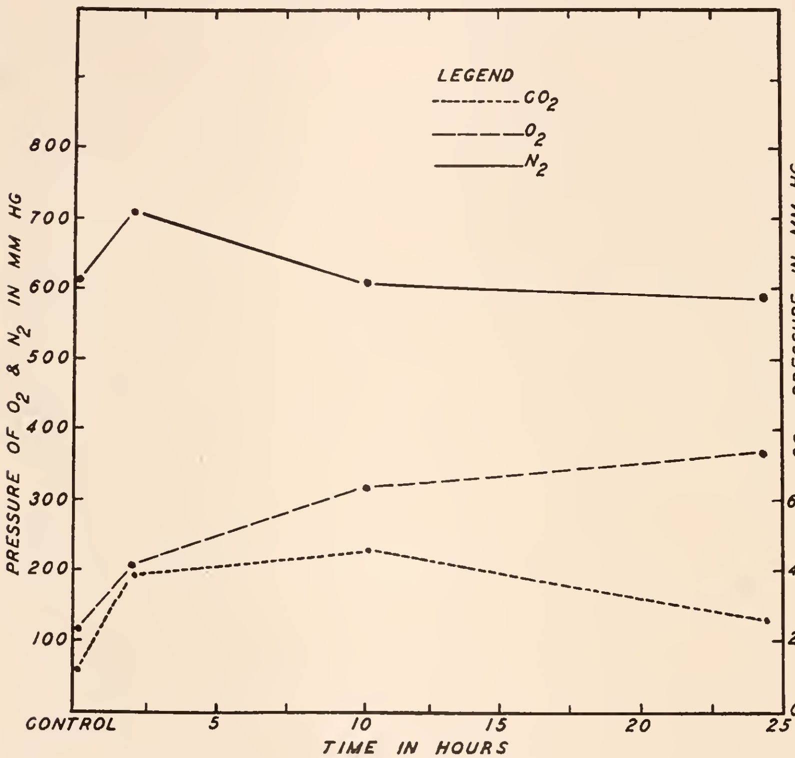

FIG. 3. A graphic representation of the data given in Table V.

oxygen which must be moved. The partial pressure of the nitrogen falls to the level of the atmospheric nitrogen by the end of the 24-hour period. Thus it can be seen that nitrogen is not deposited. Oxygen and carbon dioxide are rapidly deposited during the first two hours, and unless carbon dioxide is being removed from the swimbladder as it is being deposited, oxygen is entering the swimbladder as rapidly as

[1] Dr. Laurence Irving by personal communication.

carbon dioxide, if not more so, during the first two hours. It hardly seems likely that carbon dioxide is being removed from the swimbladder during the early part of adjustment, for, in the light of Meesters' and Nagel's and Jacob's work, carbon dioxide deposition may account for small adjustments to hydrostatic pressure. Carbon dioxide could not diffuse out of the bladder rapidly during this length of time, since it has been proved by Meesters and Nagel (1934–35) that the " oval " is tightly closed during the early part of gas deposition. Fish subjected to a total pressure of 996 mm. Hg reach hydrostatic equilibrium in 10 hours. After this time carbon dioxide partial pressure decreased toward the level of the carbon dioxide partial pressure of the control. It appears that carbon dioxide is being removed from the swimbladder after the fish have attained a state in which they are capable of moving about without too much difficulty.

In another series of experiments fish were subjected to 1417 mm. Hg for various periods of time, from 2 hours to 73.5 hours. The results of the analyses of swimbladder gas are given in Table VI, and graphically illustrated in Fig. 4, in which the partial pressures of the gases are plotted against " time " in hours. The carbon dioxide increased sharply during the first two hours from 1.54 per cent of the control to 7.98 per cent at the end of the two-hour period. During the next five hours the carbon dioxide increased to 13.93 per cent, which is the highest partial pressure recorded for this gas at the total pressure of 1417 mm. Hg. From this time, 7.5 hours, to the longest period of adjustment, carbon dioxide percentage decreased to the lowest point, 4.22 per cent, in 73 hours. This percentage is equal to a partial pressure of 59.1 mm. Hg, which is still higher than the partial pressure of this gas in the control. This indicates that, even in 73 hours, fish which have been subjected to 1417 mm. Hg of pressure have not reached a state of gaseous equilibrium within the swimbladder. It is evident that after 38 hours carbon dioxide is being removed faster than it is entering the swimbladder. The highest average partial pressure for carbon dioxide in the swimbladder of fish subjected to 1417 mm. Hg is 192 mm. Hg, and the partial pressure of CO_2 in the swimbladder of fish subjected to 2223 mm. Hg of total pressure is 197 mm. Hg. Since the carbon dioxide curve levels off at 200 mm. Hg, it might be possible that this is the limit of the amount of carbon dioxide this particular species can deposit. In other words, the level of the carbon dioxide partial pressure may be a limiting factor to the hydrostatic adjustment. The highest average partial pressure for carbon dioxide in the swimbladders of fish subjected to 996 mm. Hg is 46.1 mm. Hg. Thus it can be seen that there

Table VI

These data were obtained by the analyses of swimbladder gas taken from fish which were subjected to 1417 mm. Hg hydrostatic pressure for the duration listed in column No. 2.

No. Exp.	Time	Total Pressure	CO_2 Content	CO_2 Pressure	O_2 Content	O_2 Pressure	N_2 Content	N_2 Pressure	Temp. of Water
	hours	*mm. Hg*	*per cent*	*mm. Hg*	*per cent*	*mm. Hg*	*per cent*	*mm. Hg*	*°C.*
22	2.0	1415	8.82	122.6	36.92	513.2	54.26	754.2	26.1
22	2.0	1415	8.10	112.6	35.49	493.3	56.41	784.1	26.1
22	2.0	1415	6.04	83.9	19.20	266.9	74.16	1031.0	26.1
av.			7.98	106.3	30.53	424.4	61.61	856.4	
18	7.5	1415	13.72	190.3	30.05	416.8	56.10	778.1	28
18	7.5	1415	8.72	120.9	38.02	527.3	53.26	738.7	28
18	7.5	1415	19.17	265.9	26.87	372.7	53.93	748.0	28
av.			13.93	192.3	31.96	438.9	54.39	754.9	
17	13.7	1415	13.75	191.3	25.07	348.7	60.98	848.2	25.6
17	13.7	1415	11.06	153.8	23.67	329.3	65.27	908.3	25.6
17	13.7	1415	13.12	182.5	32.43	451.1	54.21	754.1	25.6
av.			12.67	175.8	27.09	376.3	61.14	836.9	
4	27.0	1416	13.70	196.3	30.86	430.8	55.44	773.9	22.2
4	27.0	1416	13.10	182.9	30.38	424.1	56.52	789.0	22.2
4	27.0	1416	11.10	154.5	38.44	536.6	50.86	710.0	22.2
av.			12.60	176.2	33.23	463.8	54.26	757.6	
19	38.5	1420	6.69	93.3	51.60	719.8	41.71	581.9	26.1
19	38.5	1420	13.24	184.7	46.89	655.8	39.79	565.1	26.1
19	38.5	1420	11.80	164.6	32.17	448.8	55.83	778.8	26.1
av.			10.38	147.5	43.55	606.1	45.77	641.9	
5	47.5	1414	15.27	212.8	42.24	588.8	42.23	588.7	22.2
5	47.5	1414	12.27	171.0	40.89	570.0	46.84	652.9	22.2
5	47.5	1414	2.35	32.7	56.85	792.5	40.80	576.6	22.2
av.			9.96	138.8	46.66	650.4	43.30	606.7	
10	66.0	1426	4.83	67.9	57.71	811.7	37.46	527.0	21.6
10	66.0	1226	10.06	141.4	48.90	688.0	41.04	577.3	21.6
av.			7.45	104.7	53.20	749.8	39.35	552.1	
30	73.3	1425	2.68	37.6	54.51	764.6	42.81	600.5	23.9
30	73.3	1425	8.42	118.1	42.72	598.3	48.70	683.3	23.9
30	73.3	1425	1.56	21.8	51.79	726.6	46.67	654.8	23.9
av.			4.22	59.1	49.73	696.5	46.06	646.2	

is a relationship between the partial pressure of carbon dioxide and the stimulus, the hydrostatic pressure. In the experiments carried out at 1417 mm. Hg the oxygen increased sharply during the first two hours with the initial increase in carbon dioxide, but, as in the experiments at

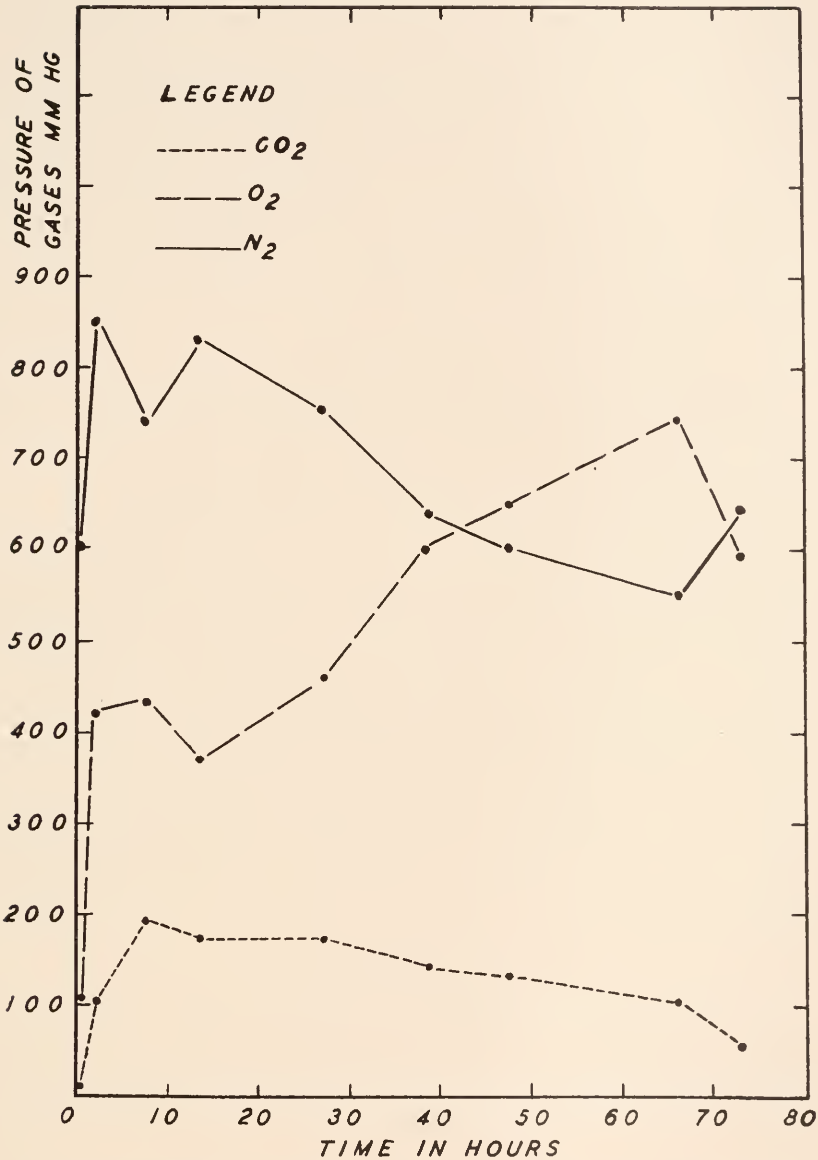

FIG. 4. A graphic representation of Table VI. The point 0 represents status of swimbladder gas of the control.

996 mm. Hg, the oxygen continued to increase after the carbon dioxide is decreasing. The nitrogen partial pressure decreases toward the level of the atmospheric nitrogen.

From these two series of experiments it is evident that both carbon dioxide and oxygen are increased sharply during the first two hours. After the fish have made a temporary adjustment to hydrostatic pressure, carbon dioxide is removed from the swimbladder faster than it is being deposited. The final adjustment results in a high partial pressure of oxygen, a carbon dioxide partial pressure near the level of the control, and a nitrogen pressure approximately equal to the atmospheric nitrogen partial pressure.

Summary

1. Rockbass were subjected to various hydrostatic pressures ranging from 540 to 2223 mm. Hg and were observed to reach a state of equilibrium at each experimental pressure.

2. Oxygen deposition accounted for half of the adjustment at the higher hydrostatic pressures.

3. After hydrostatic equilibrium had been reached carbon dioxide diffused out of the swimbladder, and the carbon dioxide percentage decreased toward the level of this gas usually found in fish at the surface of the lake. This loss in volume by the outward diffusion of carbon dioxide was compensated for by the continued deposition of oxygen.

4. Nitrogen was not deposited, and appeared to be only passively important in the adjustment to the changes in hydrostatic pressure.

5. The final adjustment to hydrostatic pressure resulted in a high partial pressure of oxygen, a carbon dioxide partial pressure near the level usually found for this gas in fish at the surface, and a nitrogen partial pressure approximately equal to the partial pressure of this gas in the atmosphere.

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